THE ARBOREAL ANCESTRY OF THE MAMMALIA.

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WITHIN the last few years Dollo and Bensley have adduced strong arguments to show that the marsupials are descended from arboreal ancestors, as indicated especially by the traces in modern marsupials of former opposability in the first digit of the manus and pes.[1] The present writer has for some time been of the opinion that this is true not only of marsupials, but of the placentals as well. Our present knowledge of fossil Mammalia and of the course of evolution of the various modern races, enables us to foreshadow with considerable detail the characters of a common ancestral group (homogeneous in adaptive characters, although perhaps embracing certain differences in dentition etc., of very ancient origin) from which all known mammals, excepting the Prototheria, are descended. That there was such a group ancestral to both metatherian and eutherian mammals is, I believe, reasonably certain. The evidence for it is the close uniformity of these Mammalia in general structure in spite of their wide divergence in adaptive specialization, and the invariable approximation towards a central type of each race whose development is known from palaeontology. As a preliminary to further discussion we may point out the characters of this primitive central type.

1.— *Size very small, skull of moderate length, brain case completely enclosed in bone, brain of high type compared with that of reptilia although lower than in the modern mammals.* In every case where we are able to trace the descent of the large modern mammals, we find their direct ancestors successively smaller as we pass backward in time. The horse and camel have been traced back nearly to the beginning of the Tertiary; their ear-

[1] This view was expressed by Huxley in 1880.

liest representatives are no larger than rabbits. Elephants, rhinoceroses, tapirs, every race about whose ancestry anything is known, exhibit a reduction in size corresponding to the distance back through which we have been able to trace them. The large animals of the early Tertiary are in every case early specializations which have left no descendants.

2.— *Molar teeth "bunodont"* i. e., *low crowned, the crowns composed of a few low broad rounded cones, heavily enamel-covered. The molars are tubercular (crushing) teeth, the premolars trenchant (cutting), the canines moderately large (piercing), the incisors small spatulate (nipping) teeth. The teeth were arranged in continuous series, except for slight gaps behind the canines.* The labors of Cope, Osborn and many other palæontologists have amply demonstrated this as the primitive type of dentition among the Mammalia. Whether we accept the whole of the Tritubercular Theory or not, this part of it appears to be beyond question.

3.— *Neck rather short, slender and flexible, permitting quick and easy turning of the head in all directions. Trunk slender, flexible, ribs rather short and few in number, lumbar region long and comparatively flexible.* These features characterize all early Tertiary mammals, without exception.

4.— *Tail very long and flexible, with strong muscles towards the base, and probably prehensible.* All primitive Tertiary mammals have remarkably long and strong tails. These differ from those of the cats and resemble those of the prehensile-tailed monkeys in the greater breadth of the zygapophyses of the proximal caudal vertebrae and great size and length of the median caudals.

5.— *Shoulder girdle of scapula and clavicle.* No indications of a separate coracoid have been observed in early Tertiary mammals, but the clavicle was certainly developed in the ancestors of several groups which do not now possess it, and was probably generally present in the earliest types.

6.— *Ilia narrow and rod-like,* gluteal muscles long and slender.

7.— *Upper members of limbs comparatively long and loosely jointed to the trunk, permitting great freedom of motion.* The

great relative length of the humerus and femur is a striking feature in the limbs of all early Tertiary mammals. In the evolution of the limbs for running the femur and humerus have generally been reduced in length and compacted into the flank, while the lower legs and feet are elongated. This places the heavy muscles high up on the limb, and by bringing its centre of gravity near to the proximal joint, enables it to swing more rapidly through a considerable arc. Thus the animal gains in length of stride without losing in quickness of step and can maintain a high speed for a long distance with less fatigue.

8. — *Ulna and radius separate, equal in size, radius with round head, permitting free supination and pronation. Tibia and fibula separate with probably more limited motion.*

9. — *Wrist and ankle very flexible, all the carpals separate and a centrale present. Astragalus with flat trochlea, distinct neck and rounded head.* This type of carpus and tarsus is found in all Basal Eocene mammals. It is retained with but little change in primates, insectivores, most rodents, and some other groups. Its gradual conversion into the various types seen in other groups is demonstrable in the Amblypoda, Condylarthra, Carnivora, partly so in the Proboscidea and Edentata, but not in the Artiodactyla and Perissodactyla which have already developed their peculiar types of astragali when they first appear in the geological record.

10. — *Five digits on each foot, the joints permitting of very free motion of fingers and toes, which were tipped by small claws.* The argument for the derivation of all mammals from pentadactyl ancestors has been fully set forth by Cope and others. The derivation of the hoofed from clawed types is likewise indicated in various lines of descent as now known.

11. — *First digit more or less opposable in both manus and pes.* This is contrary to the usual assumption that the opposable thumb found in several groups of arboreal mammals is in each case a new adaptation to their habits of life. But there is considerable evidence for it. In the first place, as far as we can trace back the history of each of the arboreal groups, we find their first ancestors with the first digit as fully opposable as in the modern representatives (*e. g.*, the Middle Eocene primate

Notharctus). Second, in those groups which have not an opposable thumb, we find as we trace back their ancestry that the trapezium, whose form and facets give the surest indication on this point, approaches more and more nearly to the type preserved in the Primates, etc. It becomes large, triangular, with very concave distal facet for the digit, and round-conical proximal faceted end abutting against the scaphoid, trapezoid and centrale. In the four Basal Eocene mammals (Pantolambda, Euprotogonia, Clænodon and Dissacus) in which this part of the skeleton is known, the form of the bone is surprisingly uniform, and when the manus is put together, the first digit is thrown partly outward from the rest of the hand, and permits of much freer motion than the remaining digits, with a considerable degree of opposition. With the development of the foot for terrestrial locomotion the trapezium and first metacarpal lose their mobility, the rounded conical proximal facet of the former separates into two flat facets at right angles for scaphoid and trapezoid, its distal facet becomes more plane and its whole distal end reduced in width and closely appressed against the proximal end of the second metacarpal, which it overlaps. In the further evolution of the running foot the first digit is reduced to a nodule and finally disappears, and the trapezium usually follows suit, the trapezoid either remaining separate (Perissodactyla) or being consolidated with the magnum (Artiodactyla).

The primitive opposability of the hallux is less clearly indicated, but the close resemblance in the form and arrangement of the internal tarsals, especially the internal cuneiform, in all early mammalia, to the intermediate stage in the evolution of the running carpus outlined above, very strongly suggests that the original condition in the tarsus was the same as in the carpus, but that its evolution for terrestrial locomotion began earlier or proceeded more rapidly.

In the third place, if we suppose, as many anatomists have done, that the so-called first metacarpal is really a proximal phalanx, and that the trapezium is the true first metacarpal, the hypothesis that all mammals passed through a stage when the pollex and hallux were opposable would supply a good reason

for the development of this anomaly, and would explain (*a*) the presence of but two phalanges on digit I, three on each of the others; (*b*) the epiphysis of digit I being proximal as in the phalanges, instead of distal as in the remaining metapodials; (*c*) the anomalous musculature of digit I on all mammals, the object of which is clearly seen when the digit is opposable, but is quite unexplained otherwise.

It would be beyond the purpose of this article to give at all fully the facts which support the above characterization of the primitive mammalia, but enough has been said to show the general nature and force of the evidence on which it is based. The modern orders of mammals have departed to a varying degree from this primitive type. The arboreal primates retain most nearly the primitive character, except that the limbs are elongated, the face is shortened and the brain greatly increased in size and complexity. The rodents, largely perhaps on account of their small size, have usually retained a great deal of the primitive skeleton character, but the dentition is much modified — least of all in the arboreal squirrels, which are almost unaltered in dental characters from the first known rodentia of the early Tertiary (Paramys, etc.). The Insectivora likewise retain many primitive characters, but in most cases in combination with one or another high specialization of an unusual kind. The Carnivora retain the primitive character more or less completely in the neck, trunk and legs, but show much greater adaptive changes in the feet and especially in the teeth. (Several of the Creodonta have a more or less opposable pollex, but this is lost in the later carnivora.) The Ungulata are by far the most highly altered group among the land mammals, almost every part of the body having gone through great adaptive changes, although the evolution is most marked in teeth and feet. We are able to trace the history of these changes more fully in this than in any other order, as its geological record is more complete. The Edentata early developed certain remarkable specializations which soon obscured their primitive characters. Of the remaining orders of placental mammals our geological record is very imperfect, and their relationship to the central type mainly hypothetical. The

marsupials, as Dollo and Bensley have shown,[1] are probably descended from an arboreal type which must have closely resembled the arboreal ancestors of the placentals, but with distinctions in the number and succession of the teeth, the origin of which is not yet clear. In these, as in the placental mammals, the modern arboreal forms are the most primitive. But it should be remembered that we know comparatively little about the palæontology of the marsupials earlier than the Quaternary, while we are able in most of the families of Ungulata, Carnivora, Rodentia and some other orders of placentals, to trace back their ancestry into the Middle or Lower Tertiary, and find them in every case converging toward the type characterized above, and quite closely converging as we come into the Basal Tertiary. We are thus enabled to place the earliest divergence from this central type in the Middle or Upper Cretaceous.

It may almost be taken for granted that if the characters of this central type were in all respects as stated above, it must have been of arboreal habitat. All its adaptations would be suitable for such a mode of life, and some would be more or less unsuitable for any other. The various modern groups (monkeys, squirrels, arboreal insectivores, opossums) which have retained this habitat are the least altered in structure, while the amount of structural change in other groups, as shown by their known palæontology, is proportioned to the change in their mode of life, the Ungulata exhibiting the greatest changes.

The hypothesis may be stated as follows :

The Cretaceous ancestors of the Tertiary mammals were small arboreal animals of very uniform skeletal characters, but probably somewhat differentiated in dentition according as fruit, seeds and nuts, or insects, formed the staple of their diet. At the beginning of the Mesozoic the available modes of life for land vertebrates were chiefly the amphibious-aquatic,

[1] A further development of the arboreal adaptation of the foot appears to have distinguished the marsupials, in the complete opposability of the hallux, with enlargement of the fourth digit and syndactyl reduction of digits II and III. It is this feature that is regarded by these authors as especially indicating arboreal habits.

the arboreal and the aerial, the terrestrial habitat being subordinate because the upland Flora was largely undeveloped or inedible as compared with its present condition. The three available provinces were occupied by reptiles, mammals and birds respectively. In the later Cretaceous the spread of a great and varied upland flora vastly extended the terrestrial province, and opened a new and constantly widening field for the expansion of the mammalia. These then commenced a great evolution, the new terrestrial groups expanding continually and becoming adapted to various modes of life. The arboreal types maintained or increased their lead in intelligence, but changed comparatively little in other respects. The terrestrial types became far more numerous and dominant, adapting their primitively arboreal organization to their various modes of life, yet retaining, in spite of extensive changes, a certain fixity of type which had been impressed upon them by their long arboreal residence.

The great extension of the terrestrial province in the Tertiary may be supposed to have opened a correspondingly large field for the expansion of the birds, but these, retaining in the main their aerial life, suffered but little change in organization, and the vast majority are today as homogeneous in skeleton structure as the mammals were at the beginning of the Tertiary. Coincident with the expansion of the terrestrial province was a great contraction of the amphibious-aquatic province. The extensive swamps and deltas and great inland seas of the Cretaceous, shrank at its close to small proportions, and the Reptilia underwent a corresponding diminution, some groups completely disappearing, others surviving through the Tertiary in continually decreasing numbers, the land reptiles (lizards and snakes) alone prospering. Both birds and reptiles, so far as they have retained their typical habitats, have changed but little structurally since the Mesozoic; only the few terrestrial reptiles and terrestrial or aquatic birds show an amount of change comparable with that in the terrestrial mammalia. It would seem therefore that all the facts accord with the explanation of the evolution of mammals during the Cenozoic as caused by their invasion of a new province and change of habitat from arboreal to dominantly terrestrial.

The little that is known of the Mesozoic Mammalia fits in with our hypothesis of their arboreal habitat but adds little to the evidence in its favor. Practically nothing is known of their skeletal structure; they are all of small or minute size, with teeth of insectivorous or granivorous type. They have been referred to monotremes, marsupials and insectivores, in each case on very insufficient evidence, but their ordinal relationships have little to do with the question of their habitat and need not be considered here. Their minute size, and association, in strata of fresh or brackish water origin, with large amphibious and aquatic reptiles and with abundance of fossil wood, suggest that the deposits in which they occur were laid down in extensive forest-clad river deltas and coastal swamps, and that the minute mammalia represent the arboreal fauna of these forests.

I am not well acquainted with the embryologic evidence which might bear upon the hypothesis advocated in this paper. Most investigations into mammalian ontogeny have had other problems in view. The deviation of placentals from marsupials or vice versa, and the ultimate origin of the mammalia from amphibian or reptilian ancestors, do not directly affect the question of the habitat of the Mesozoic ancestors of the Tertiary mammals. But undoubtedly important evidence on this point could be obtained from the ontogeny of their modern descendants, although not, perhaps, of the same force as the more direct evidence from palæontology.

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